

Spectral Sensitivity of Vertically Migrating Marine Copepods

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Abstract. Light is a critical factor in the proximate basis of diel vertical migration (DVM) in zooplankton. A photo-behavioral approach was used to examine the spectral sensitivity of four coastal species of calanoid copepod, representing a diversity of DVM patterns, to test whether species that migrate (nocturnal or reverse DVM) have response spectra that differ from non-migratory surface dwellers. The following species were given light stimuli at wavelengths from 350 to 740 nm, and their photoresponses were measured: *Centropages typicus* (nocturnal migrator), *Calanopia americana* (nocturnal migrator), *Anomalocera ornata* (reverse migrator), and *Labidocera aestiva* (non-migrator). *Centropages typicus* and *A. ornata* had peak responses at 500 and 520 nm, respectively, while *Calanopia americana* had maximum responses at 480 and 520 nm. Thus, the species that undergo DVM have peak photobehavioral responses at wavelengths corresponding to those available during twilight in coastal water, although the range of wavelengths to which they respond is variable. Non-migratory surface-dwelling *L. aestiva* had numerous response peaks over a broad spectral range, which may serve to maximize photon capture for vision in their broad-spectrum shallow-water habitat.

Introduction

Diel vertical migration (DVM) is an extremely common pattern of vertical movement in the water column that occurs in both freshwater and marine zooplankton, particularly the copepods (Haney, 1988; Longhurst and Harrison, 1989). Of the three general DVM patterns that have been recognized, the most common is an ascent in the water

column to minimum depth around sunset and descent to maximum depth around sunrise, termed nocturnal, or normal, DVM. Another pattern, reverse DVM, involves an ascent to shallow water at sunrise followed by a descent to deeper water at sunset. The third pattern, twilight DVM, involves an ascent to the surface at sunset, a descent to deeper water around midnight (*i.e.*, the “midnight sink”), followed by a second ascent to the surface and then descent to deeper water at sunrise. There is variability in which pattern is expressed for any given species at a particular place and time (*e.g.*, Bollens and Frost, 1989; Ohman, 1990).

The hypothesis for the ultimate evolutionary advantage of DVM that finds the most support in the literature is that of reduced mortality risk by predator avoidance (*e.g.*, Frost, 1988; Bollens and Frost, 1989; De Robertis *et al.*, 2000). Accordingly, nocturnal and twilight DVM provide both a daytime refuge from visual predation in dim light areas at depth and nighttime access to food-rich surface waters. Reverse DVM provides protection from nocturnally migrating predators (Ohman *et al.*, 1983). The proximate physiological mechanisms thought to control the movement of migrators during DVM involve aspects of the diel light cycle (for reviews of competing hypotheses, see Forward, 1988; Ringelberg, 1999). Some of the strongest evidence for the role of light in DVM comes from field observations that (1) migration usually occurs at twilight, which is the time of day with the greatest relative change in irradiance, and (2) some zooplankton species maintain their depth at distinct levels of irradiance throughout the diel cycle (*e.g.*, Frank and Widder, 2002). Laboratory observations also suggest that many zooplankton species have behavioral responses to relative rates of irradiance change that are consistent with swimming during DVM. Furthermore, photophysiological thresholds for these responses tend to correlate with relative

Received 13 August 2002; accepted 9 October 2002.

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rates of irradiance change occurring at twilight at depths inhabited by migrating zooplankton (Forward, 1988; Ringelberg, 1995).

The spectral distribution of light underwater has been well studied and is determined by a combination of the ambient skylight and the optical properties of seawater, with its associated biological materials (e.g., phytoplankton and colored dissolved organic matter). Light becomes increasingly monochromatic with depth; the color is determined by those wavelengths that are attenuated less as they pass into deep water (Jerlov, 1976). Estuarine waters transmit maximally at longer wavelengths (~580 nm), whereas coastal waters transmit better at slightly shorter wavelengths (~500 nm), and clear ocean water transmits best at even shorter wavelengths (~470 nm). Even though UVA (320–400 nm) is attenuated more than blue-green light, a substantial amount is present underwater (Losey *et al.*, 1999). Downwelling irradiance at 380 nm, measured offshore of Beaufort Inlet, North Carolina, at high tide in both spring and fall, was about 10^{15} photons $m^{-2} s^{-1}$ at depths of 10 and 13 m, respectively (water column depths 17 and 24 m; NOAA Coastal Remote Sensing Program, <http://www.csc.noaa.gov/crs>). Given these data for water close to an estuary (Newport River Estuary, NC), there is likely to be adequate long-wavelength UVA light for visual perception over most depths in relatively clearer coastal habitats.

Studies on fish vision have yielded two hypotheses concerning how the spectral sensitivity of visual pigments relates to the spectral quality of light in an organism's habitat. The contrast hypothesis states that wavelength sensitivity is either matched to or offset from ambient wavelengths, depending on depth of habitat and line of sight, in order to maximize contrast between an object and the background (Lythgoe, 1968; McFarland and Munz, 1975). Alternatively, the sensitivity hypothesis suggests that the wavelength sensitivity of visual pigments is matched to the ambient wavelengths present in the environment, in order to maximize photon capture (Munz, 1958; Partridge and Cummings, 1999). Forward (1988) suggested that the spectral sensitivity hypothesis holds for the few species of vertically migrating zooplankton that have been studied; but rather than being adapted to maximize photon capture during the day, these organisms have spectral sensitivities matched to the ambient light during times of vertical migration (i.e., twilight). At twilight, there is a relative reduction in the spectral region of 540–625 nm (yellow) and increases near 500 (blue-green) and 680 nm (red). This phenomenon is termed the Chappuis effect, and is particularly prominent near the surface in coastal regions (Hobson *et al.*, 1981). However, Forward *et al.* (1988) reported that the Chappuis effect was detectable in April near the bottom (2.5 m) of the relatively turbid Newport River Estuary in North Carolina. Given the spectral transmission of estuarine and coastal water, coupled with the Chappuis effect, zooplankton that

undergo DVM in these regions will likely be adapted to respond maximally to light at 480–520 nm (Forward, 1988).

The purpose of the present study was to determine whether there are differences in the spectral sensitivities of four coastal species of calanoid copepod (*Centropages typicus*, *Calanopia americana*, *Anomalocera ornata*, and *Labidocera aestiva*) that differ in their reported DVM behaviors. Both *Centropages typicus* and *Calanopia americana* undergo nocturnal DVM (Clarke, 1933, 1934; Bowman, 1971; White *et al.*, 1979). *A. ornata* is a reverse migrator (P. Tester, NOAA Coastal Ocean Program, pers. comm.), and *L. aestiva* is a non-migratory surface dweller (Wilson, 1932; Turner *et al.*, 1979). We hypothesized that the non-migratory species that inhabits surface waters during the day (*L. aestiva*) would be responsive to a wide range of wavelengths in order to maximize photon capture for daytime vision in its broad-spectrum habitat. Conversely, vertically migrating species (*Centropages typicus*, *Calanopia americana*, and *A. ornata*) were predicted to be responsive to a narrow range of wavelengths matched to those occurring at depth in their coastal habitat, particularly at twilight (480–520 nm; Forward *et al.*, 1988). Of the four species tested, the non-migratory surface-dwelling *L. aestiva* responded to the greatest range of wavelengths. The nocturnal migratory species *Centropages typicus* and *Calanopia americana*, as well as the reverse migrator *A. ornata*, were maximally responsive to blue-green light (~500 nm), but the range of wavelengths over which they responded was variable.

Materials and Methods

Centropages typicus, *Calanopia americana*, and *Labidocera aestiva* were captured using a stationary 0.75-m plankton net with a mesh size of 333 μm . The net was set prior to maximum current on nighttime flood tides near Beaufort Inlet, North Carolina (34°4'N, 76°41'W). Nets set at this time ensured high densities of these species. *Anomalocera ornata* was captured with the same net during daytime surface tows ~24 km offshore of Beaufort Inlet. Although this species did occur in daytime plankton samples collected inshore, it was more abundant offshore. Salinity in Beaufort Inlet and surrounding areas usually ranges from 30 to 36 ppt. All net samples were diluted with ambient seawater, brought to the laboratory, and allowed to acclimate for at least 4 h to the temperature of all experiments (23 °C).

No longer than 12 h after collection, plankton were sieved twice (3.2 mm and 0.7 mm) to remove macroplankton and macroalgae. Adult female copepods were identified to species and sorted under a dissecting microscope (Fleminger, 1956; Lawson and Grice, 1970; F. Ferrari, Smithsonian Institution, pers. comm.). Groups of copepods were gently pipetted into 40 ml of aged 100-kDa-filtered offshore seawater (36 ppt), in which they remained without food until use in an experiment (no longer than 3 h). Preliminary

experiments indicated that photoresponses of unfed copepods remained constant over this time period.

Aged 100-kDa-filtered seawater was prepared by septic filtration (A/G Technology Corp. model UFP-100-C-4X2A) of offshore seawater to remove biologically active molecules larger than 100 kDa, and subsequent aging for at least 1 week. This process produces seawater with a consistent chemical composition that does not alter crustacean photoresponses (Rittschof *et al.*, 1983; Forward and Rittschof, 2000). Since chemical cues from fish predators can alter zooplankton photoresponses involved in DVM (*e.g.*, Forward and Rittschof, 2000), the potential effects of these chemical cues were removed by incubation in the 100-kDa-filtered seawater.

Groups of copepods (90 *Centropages typicus*, 90 *Calanopia americana*, 40 *A. ornata*, and 50 *L. aestiva*) were transferred to a transparent acrylic cuvette (3 × 3 × 5 cm for *Centropages typicus*, *Calanopia americana*, and *L. aestiva*; 5 × 5 × 5 cm for *A. ornata*) filled with 100-kDa-filtered seawater, and dark adapted for at least 1 h prior to spectral sensitivity testing. The number of copepods in a group was inversely proportional to copepod body size. Five replicate groups of each species were tested. Stimuli were presented in increasing order of wavelength, spanning UVA, visible, and far-red light (350–740 nm). Each stimulus lasted 5 s, with 3 min of dark adaptation provided between successive stimuli. A group of copepods received the entire stimulus series, and was then discarded. Preliminary experiments indicated that the order of the stimuli did not alter the response, as repetition of a 500-nm stimulus after the entire stimulus series resulted in a response similar to that observed during the initial 500-nm stimulus for each species. In addition, copepods showed consistent photoresponses upon repeated stimulation at 500 nm with 3 min provided between stimuli, suggesting that the 3-min time interval was sufficient to return the animals to the level of dark adaptation they had prior to the initial stimulus. Copepods resumed pre-stimulus (normal) swimming behavior within 30 s after termination of a stimulus. All experiments were conducted between 0900 and 1700 h to reduce the potential effect of an endogenous rhythm on photobehavior.

A 400-W quartz-tungsten-halogen filament lamp (Oriental housing model 6140-I), fitted with a deionized water filter to remove heat, was used to provide light stimuli. Light from the lamp was focused, using a plano convex lens, onto the 20-nm entrance slit of a grating monochromator (Oriental model 7240). Spectral purity of the monochromator was enhanced by using blocking filters: Corning No. 7–54 for the UVA region, No. 4–96 for the blue-green region, and No. 3–67 for the yellow-red region. Light of a desired waveband emitted from the 12-nm exit slit of the monochromator was collimated and focused through fixed neutral-density filters to control irradiance and onto an electromagnetic shutter (Uniblitz model 300-B) to control stimulus

duration. When the shutter was opened, light was allowed to pass through a light-tight shield and into a dark room. Light was reflected off two front-surface mirrors and down into the cuvette containing copepods. All optics were composed of fused silica to transmit UVA.

To control for variation in irradiance among wavelengths due to the emission spectrum of the lamp and transmission from the monochromator/blocking filters, fixed neutral-density filters were used to achieve an equivalent irradiance value at all wavelengths (EG & G model 550 radiometer). In initial experiments examining photoresponse *versus* irradiance at 500 nm, approximate photoresponse thresholds were determined. Experimental irradiance values above this threshold could then be set at levels that were neither too high nor too low for eliciting responses in each species. This procedure helped to account for differences in the absolute photosensitivity among the test species. *Centropages typicus*, *A. ornata*, and *L. aestiva* had photoresponses as low as 1×10^{13} photons $\text{m}^{-2} \text{s}^{-1}$, with distinct responses observed at 1×10^{14} photons $\text{m}^{-2} \text{s}^{-1}$. *Calanopia americana* had greater absolute photosensitivity, with photoresponses as low as 1×10^{12} photons $\text{m}^{-2} \text{s}^{-1}$ and distinct responses observed at 1×10^{13} photons $\text{m}^{-2} \text{s}^{-1}$. Accordingly, for spectral sensitivity experiments, the irradiance level for each test wavelength was controlled arbitrarily at 1 log unit above the apparent threshold for each species. The most recent accounts of vertical distributions of these species (Bowman, 1971; Turner *et al.*, 1979; White *et al.*, 1979; P. Tester, NOAA-COP, pers. comm.) have been studied only to identify DVM pattern and were not related to ambient light levels. Thus, it is likely that the irradiance values used in the experiments are somewhat lower than those the animals would be exposed to during the day in their coastal habitat. PAR (photosynthetically active radiation, 400–700 nm) values of 5×10^{20} photons $\text{m}^{-2} \text{s}^{-1}$ (2-m depth) and 6×10^{19} photons $\text{m}^{-2} \text{s}^{-1}$ (13-m depth) were measured at high tide offshore of Beaufort Inlet, North Carolina, at 1200 h (24-m water column depth, 13 March 1997; NOAA Coastal Remote Sensing Program, <http://www.csc.noaa.gov/crs>). Accordingly, experimental irradiance levels were probably 5–6 orders of magnitude lower than the daytime levels for the species tested.

Movement of copepods during the experiments was recorded using a closed-circuit video system with near-infrared illumination (maximum transmission = 774 nm), which does not alter or induce crustacean photoresponses (Forward and Cronin, 1979). Aspects of swimming behavior and orientation were later analyzed from video recordings either by hand (*L. aestiva* only) or using a PC-based motion analysis system (CellTrak software, Motion Analysis, Inc.). Swimming behavior was analyzed during the middle 4 s of each 5-s stimulus (response), as well as 10 s prior to each stimulus for the same duration in the dark (control).

The species tested exhibited very different photobehav-

iors from one another; therefore it was necessary to analyze different aspects of swimming behavior for each species. For *Calanopia americana*, which was strongly phototactic, positive phototaxis was analyzed. The mean angular direction of movement in the XY-plane for copepods in the field of view (~25 individuals) was determined from digitized video recordings using CellTrak software. Only animals that oriented in a significant direction were used for analysis (Rayleigh's z , $\alpha = 0.01$). The percentage of copepods swimming upward toward the stimulus light $\pm 30^\circ$ (positive phototaxis) was determined. An increase in the percentage of copepods exhibiting positive phototaxis relative to the control values indicated increased responsiveness to light, whereas a decrease in responsiveness was indicated by a decreased percentage of positive phototaxis.

Centropages typicus was not phototactic, but did exhibit a hop-sink swimming pattern in the dark and a linear swimming pattern with no distinct directional pattern when stimulated with light. Accordingly, an estimate of path linearity, the net-to-gross displacement ratio (NGDR), was analyzed using CellTrak software. NGDR is calculated as the ratio of the net-to-gross displacement of a copepod during the 4-s analysis interval. Net displacement is the distance along a straight line from the starting point of a copepod's path of travel to the ending point. Gross displacement is the distance along the path the copepod traveled over the same time period. NGDRs were calculated for individual copepods in the field of view (~15 individuals) and averaged to obtain stimulus and control NGDR values. An increase in the stimulus NGDR relative to the control value indicated increased responsiveness, whereas a decrease indicated decreased responsiveness.

A. ornata was not phototactic. In the dark it exhibited position maintenance with oscillating vertical swimming about a central point; when stimulated with light it responded with linear movement. For this species, the rate of change in direction (RCD) was analyzed. RCD is calculated as the absolute value of the angular velocity measured for every point in the path traveled by a copepod over the 4-s analysis interval and averaged for the path. RCD values for all copepod paths in the field of view (~15 copepod paths) were averaged to obtain stimulus and control RCD values. A decline in stimulus RCD value relative to control values indicated an increase in linear swimming and responsiveness; an increase in the RCD index indicated oscillating swimming and decreased responsiveness.

L. aestiva did not exhibit phototaxis, but did demonstrate a dorsal light reflex, which was described by Land (1988). The percentage of copepods in the field of view (~15 individuals) undergoing a dorsal light reflex (frontal axis perpendicular to the stimulus light $\pm 30^\circ$) was analyzed. An increase in the percentage of copepods that displayed this response relative to control values indicated increased re-

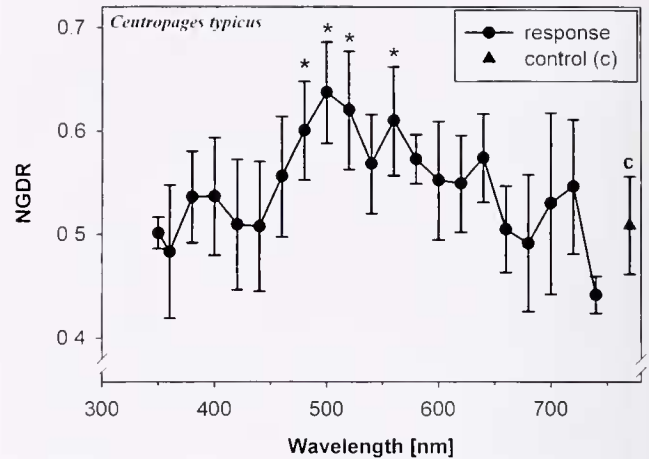


Figure 1. Spectral sensitivity of *Centropages typicus*. The ratio of net-to-gross displacement (NGDR) is plotted as a function of wavelength. Circles connected with a solid line represent the mean response value (\pm SE) for five trials at each wavelength stimulus. The triangle represents the mean control (c) value (\pm SE) calculated by pooling dark controls for all wavelength stimuli in five trials. Asterisks denote significant differences ($P < 0.05$) between the mean response and the pooled control using a one-factor repeated measures ANOVA with a Dunnett's test for multiple comparisons ($q'_{0.05(1)}$ 84,22, Zar, 1999).

sponsiveness; decreased responsiveness was indicated by a decreased dorsal light reflex percentage.

A one-factor repeated measures (RM) ANOVA for each species indicated that there were no differences in the dark control values prior to the stimuli ($P > 0.05$; Zar, 1999). Accordingly, the control values for each wavelength stimulus were pooled, yielding a single mean control and standard error for each species. Response data were then analyzed for each species by using a one-factor repeated measures ANOVA, including the control as an additional treatment. Multiple comparisons were done using a Dunnett's test versus the control treatment ($q'_{0.05(1)}$ 84,22; Zar, 1999). A one-tailed statistical test was used because light stimulation was expected to change the response variable in a predictable direction relative to the control (increases for *Centropages typicus*, *Calanopia americana*, and *L. aestiva*; decreases for *A. ornata*).

Results

The nocturnally migrating *Centropages typicus* responded to few wavelength stimuli (Fig. 1). NGDR values significantly greater than the control value were observed between 480 and 560 nm, with a sensitivity peak at 500 nm (one-factor RM ANOVA, $P = 0.03$; Dunnett's test, $P < 0.05$). Responsiveness was not significant at wavelengths both shorter and longer than this blue-green region (Dunnett's test, $P > 0.05$).

In contrast, the other nocturnally migrating species tested, *Calanopia americana*, responded to many wavelength stimuli

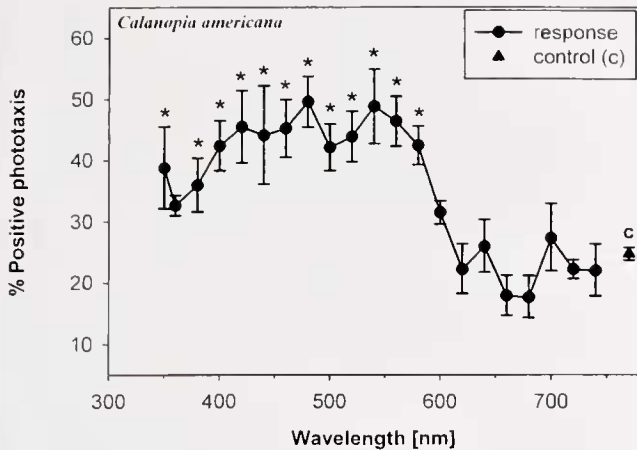


Figure 2. Spectral sensitivity of *Calanopia americana*. The percentage of copepods displaying positive phototaxis (upward swimming $\pm 30^\circ$) is plotted as a function of wavelength. All other symbols are as described for Figure 1.

(Fig. 2). Positive phototactic responses significantly greater than the control value were found in the UVA (350, 380, 400 nm), with even greater response values from 420 to 580 nm (one-factor RM ANOVA, $P < 0.001$; Dunnett's test, $P < 0.05$). No significant phototactic response occurred at wavelengths above 580 nm (Dunnett's test, $P > 0.05$).

The reverse migrator, *Anomalocera ornata*, was similar to *Centropages typicus* in that it also responded to few wavelength stimuli (Fig. 3). RCD index values were significantly less than the control value in the spectral region between 460 and 540 nm, with a sensitivity peak at 520 nm (one-factor RM ANOVA, $P < 0.001$; Dunnett's test, $P < 0.05$). Wavelength stimuli outside of this narrow spectral region did not elicit a significant response (Dunnett's test, $P > 0.05$).

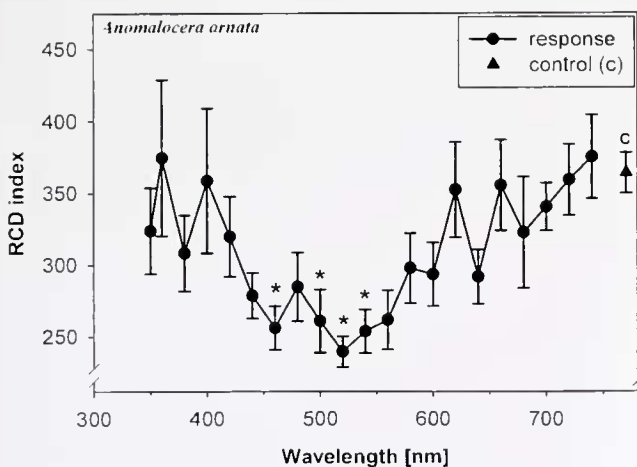


Figure 3. Spectral sensitivity of *Anomalocera ornata*. The index of rate of change in direction (RCD) is plotted as a function of wavelength. All other symbols are as described for Figure 1.

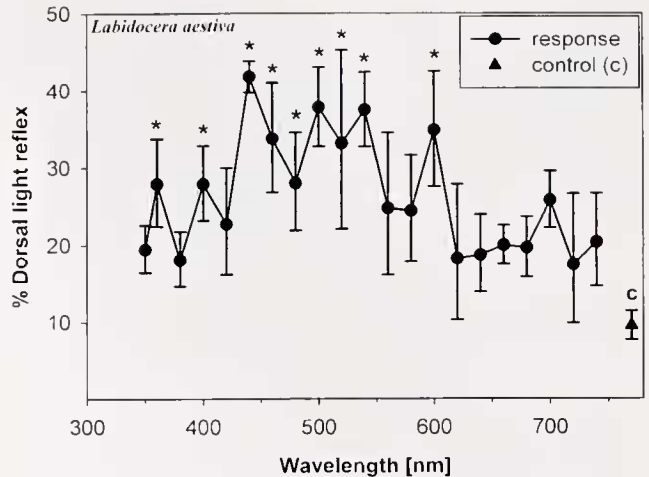


Figure 4. Spectral sensitivity of *Labidocera aestiva*. The percentage of copepods displaying the dorsal light reflex (frontal axis perpendicular to the stimulus light $\pm 30^\circ$) is plotted as a function of wavelength. All other symbols are as described for Figure 1.

The surface dwelling *Labidocera aestiva* responded to all wavelength stimuli tested with a higher mean percentage of individuals undergoing a dorsal light reflex than in the dark control (Fig. 4). Peak significant responses occurred at 440–540 and 600 nm in the visible, with minor peaks at 360 and 400 nm in the UVA (one-factor RM ANOVA, $P = 0.005$; Dunnett's test, $P < 0.05$).

Discussion

We hypothesized that *Labidocera aestiva*, a non-migratory species that inhabits broad-spectrum surface waters during the day, would be responsive to the widest range of wavelengths. We predicted that the nocturnal migrators *Centropages typicus* and *Calanopia americana*, as well as the reverse migrator *Anomalocera ornata*, would have photoresponses over relatively fewer wavelengths, specifically those matched to the ambient wavelengths that occur at twilight in their coastal habitat (480–520 nm). These predictions were verified for all species except *Calanopia americana*, which had photoresponses over a greater range of wavelengths than was expected.

An alternative explanation for the observed interspecific differences in the location and range of spectral sensitivities is that spectral sensitivity relates to the specific behaviors analyzed. While the use of different response variables for each species is not ideal for making interspecific comparisons, the distinctly different behaviors exhibited by each copepod species when exposed to light precluded the use of any one variable to quantify copepod photoresponses. Although no independent direct comparison is available for all the response parameters used here to quantify photobehavior, several studies have analyzed photobehavior with com-

binations of these parameters or used a single parameter to compare species. Buskey *et al.* (1995) used rate of change in direction (RCD) and the net-to-gross displacement ratio (NGDR) simultaneously as parameters to quantify swarming photobehavior of the copepod *Dioithona oculata* around light shafts that differed in irradiance. Both parameters yielded the same values for the irradiance at which swarming photobehavior occurs. Two studies have used phototaxis as a response variable to examine the spectral sensitivity of marine copepods (*Acartia tonsa*, Stearns and Forward, 1984; *Pleuromamma xiphias* and *P. gracilis*, Buskey *et al.*, 1989). These species all showed phototaxis as a behavioral response to light, but they responded to light stimuli with different orientation directions, and with distinct differences in spectral sensitivity. *A. tonsa* had positive phototactic responses, with sensitivity from 453–620 nm; *P. xiphias* and *P. gracilis* both had negative phototactic responses, with sensitivity from 460–540 nm and 420–620 nm, respectively. These studies demonstrate that copepods vary in their behavioral responses to light stimuli, as was also observed in the present study, and that even when the same behavioral response parameter is used (*e.g.*, phototaxis), there is variability in the observed spectral sensitivity.

Labidocera aestiva responded well to wavelengths that transmit best in coastal water (~500 nm); yet it also responded to longer and shorter wavelengths, including those in the UVA. Responsiveness to such a wide range of wavelengths suggests that this surface-dwelling species may be capable of utilizing the broad-spectrum light available at shallow depths to maximize photon capture for daytime vision. *L. aestiva*, like many pontellid copepod species, has highly modified lens eyes and is capable of complex visual behaviors (Vaissière, 1961; Land, 1988). Feeding may represent an important visual task for this species, which is a raptorial predator that relies on its ability to detect and grasp relatively large motile prey items (including copepod nauplii) from the water column rather than exclusively using a suspension-feeding current (Turner, 1984; Conley and Turner, 1985). Aquatic organisms, particularly planktivorous fishes, may utilize UVA wavelengths to visualize opaque and transparent zooplankters (reviewed by Johnsen, 2001). The UVA photoresponses we observed for *L. aestiva* suggest that this surface-dwelling predatory zooplankter could employ a mechanism of UVA-enhanced prey detection.

Of the species we tested that are known to undergo DVM, only *Centropages typicus* (nocturnal migrator) and *A. ornata* (reverse migrator) had spectral sensitivities limited to a narrow range of wavelengths. Their responses peaked between 500–520 nm, so these copepods are well suited for maximizing photon capture in coastal waters, particularly at twilight when—because of the Chappuis effect—blue-green wavelengths dominate the coastal ambient light spec-

trum. As has been suggested for other zooplankton that undertake vertical migrations at twilight (*e.g.*, Forward, 1988; Forward *et al.*, 1988), their spectral sensitivity matches the ambient wavelengths during a time period when light is a critical environmental cue for orienting and controlling DVM behavior. Interestingly, *A. ornata* has a distinctive blue-green pigmentation (Herring, 1965), and has the highly developed eyes characteristic of the pontellids (*e.g.*, Vaissière, 1961). The coloration presumably confers some protection from predators and photodamage during its daytime residence in surface waters, and the eye may be involved in complex visual behaviors. It is intriguing to speculate that the photoresponsiveness *A. ornata* showed to blue-green wavelengths may relate to the visual detection of pigmented conspecifics, although further study is needed for verification.

Like *Centropages typicus* and *A. ornata*, the nocturnally migrating oceanic species *Pleuromamma xiphias* has photobehaviors limited to blue-green wavelengths (460–540 nm; Buskey *et al.*, 1989). A distinct difference between the coastal species in the present study and the oceanic one is that the sensitivity maximum for the oceanic copepod is shifted to shorter wavelengths. The sensitivity maximum for *P. xiphias* was 480 nm, whereas sensitivity maxima for *Centropages typicus* and *A. ornata* were 500 and 520 nm, respectively. This difference is consistent with the characteristic shift in the spectral transmission of seawater to longer wavelengths in coastal regions relative to oceanic ones; the shift is due to greater amounts of phytoplankton and suspended organic material nearshore.

While the other vertically migrating species we tested, *Calanopia americana*, had maximum responses at 480 and 520 nm, we also observed significant photoresponses at both longer and shorter wavelengths, including the UVA. Instead of being adapted to respond to only a narrow range of ambient twilight wavelengths, this species has a sensitivity maximum in the green spectral region (550 nm), but is equally responsive to shorter wavelengths that would be present at twilight (480 nm). *Calanopia americana* is a very strong nocturnal vertical migrator (Clarke, 1934), and has also been documented to undergo a seasonal shift in distribution off the coast of North Carolina. Bowman (1971) reported that the species was abundant inshore during the summer and fall, but was found mainly at shelf and oceanic stations during winter and spring. The observed spectral sensitivity of *Calanopia americana* suggests that its photobehaviors are well suited for ambient wavelengths offshore, as well as for the relatively longer wavelengths that dominate the inshore light environment. A similarly wide spectral sensitivity (453–620 nm) was previously observed using a similar phototaxis assay for *Acartia tonsa*, a copepod that undergoes nocturnal DVM and is common in both estuarine and shelf waters (Stearns and Forward, 1984).

Knowledge of the spectral absorption characteristics of photopigments for vertically migrating organisms and their relationship to the spectral availability of ambient light is critical to understanding the proximate physiological basis of DVM. Information on the photoresponsiveness of migrators to UV and visible wavelengths is necessary for making appropriate underwater light measurements to be correlated with behavioral movements of migrating organisms (Clarke, 1933; Widder and Frank, 2001). Behavioral observations in this study demonstrate that vertically migrating and non-migrating species of calanoid copepod from the same coastal habitat differ in their spectral sensitivities. Copepods that undertake either nocturnal or reverse vertical migrations are maximally responsive to wavelengths corresponding to those available during twilight, although the range of wavelengths over which they respond is variable. Non-migrating copepods that occur near the surface respond to a greater spectral range that is better suited for maximizing photon capture in broad-spectrum surface waters.

Acknowledgments

This material is based in part on research supported by the National Science Foundation grant OCE-0095092 to RBF. The manuscript was improved by the helpful comments and suggestions of two anonymous reviewers.

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